# Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and Pacific silver fir ecosystems in western Washington

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Decomposition rates and changes in the nutrient content of needle and leaf litter were examined in Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), and red alder (*Alnus rubra* Bong.) ecosystems in western Washington, U.S.A. Nylon litterbags (1-mm mesh) were placed in the stands in November and December 1974. Bags were collected after 3, 6, 12, and 24 months and weighed, except in the Pacific silver fir stand when bags were collected after 6, 9, 14, and 24 months. Litter was analyzed for C, N, P, K, Ca, Mg, Mn, lignin, and cellulose. Decomposition constants (*k* values) were determined. Fastest decomposition after 2 years occurred in red alder leaves, followed by Douglas-fir, western hemlock, and Pacific silver fir needles. There were significant differences in weight loss among species after 1 year, but no significant differences were evident after 2 years. Red alder leaves showed rapid weight loss in the 1st year but decomposed little in the 2nd year. Decomposition constants were highly positively correlated with minimum air temperatures and negatively correlated with C:N ratios. Low litter moisture tended to reduce decomposition in summer, particularly in the Pacific silver fir stand. Decomposition proceeded under snow in this ecosystem. The pattern of loss of elements from litterbags after 2 years varied from ecosystem to ecosystem, particularly for N. The following element mobility series resulted for the four ecosystems: red alder (K > Mg > Ca > P > N > Mn), Douglas-fir (K > P > Ca > Mg > Mn > N), western hemlock (K > Ca > Mg > N > Mn > P), and Pacific silver fir (K > Mg > Ca > Mn > P > N).

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L'auteur a étudié le taux de décomposition et les changements de contenu en éléments nutritifs des litières d'aiguilles et de feuilles dans des peuplements de *Pseudotsuga menziesii* Mirb. Franco, de *Tsuga heterophylla* (Raf.) Sarg., d'*Abies amabilis* (Dougl.) Forbes, et d'*Alnus rubra* Bong., dans la partie ouest de l'Etat de Washington, U.S.A. A cette fin, il a utilisé la technique des sachets en nylon (mailles de 1 mm) placés au sol, en novembre et décembre 1974, et renfermant la litière. Les sachets furent prélevés après 3, 6, 12 et 24 mois et subséquemment pesés; dans le cas du peuplement d'*A. amabilis*, les prélèvements eurent lieu après 6, 9, 14 et 24 mois. La litière fut analysée pour sa teneur en C, N, P, K, Ca, Mg, Mn, ainsi que sa teneur en lignine et en cellulose. Les constantes (*k*) de décomposition ont ainsi été déterminées. La décomposition la plus rapide après 2 ans s'est produite chez les feuilles d'*A. rubra,* suivi des aiguilles de *P. menziesii, T. heterophylla* et *A. amabilis.* Les différences de pertes de poids entre les espèces étaient significatives après un an, mais non après 2 ans. Les feuilles d'*A. rubra* ont accusé une perte rapide de poids la 1ère année, mais faible au cours de la 2$^e$ année. Les constantes de décomposition étaient en corrélation positive étroite avec les températures minimales de l'air et en corrélation négative avec les rapports C:N. Une faible teneur en humidité s'est traduite par une décomposition ralentie en été, surtout dans le peuplement d'*A. amabilis.* La décomposition s'est poursuivie sous la neige dans cet écosystème. La distribution des pertes d'éléments de la litière après deux ans variait d'un peuplement à l'autre, en particulier pour N. Les séries de mobilité suivantes ont été observées pour les quatre peuplements: *A. rubra* (K > Mg > Ca > P > N > Mn); *P. menziesii* (K > P > Ca > Mg > Mn > N); *T. heterophylla* (K > Ca > Mg > N > Mn > P); *A. Amabilis* (K > Mg > Ca > Mn > P > N).

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## Introduction

Few litter decomposition studies have been conducted in the United States Pacific Northwest forests despite the economic importance of these forests. Fogel and Cromack (1977) examined Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) needle decomposition in old-growth forests, and Edmonds (1979) determined Douglas-fir needle decomposition rates in an age sequence of stands less than 100 years old. More recently, Fogel and Hunt (1979) studied needle and fine root decomposition in a young Douglas-fir stand and Vogt et al. (1980) examined litter decomposition in other forest types. Only in my previous study (Edmonds 1979) was nutrient release from decomposing litter considered.

This study was initiated to determine needle and leaf decomposition and subsequent nutrient release in four typical Pacific Northwest forest ecosystems. The specific objectives of the study were to (1) determine the rates of decomposition of litter and the factors controlling them in one deciduous and three coniferous ecosystems, (2) examine seasonal patterns of decomposition, and (3) determine patterns of release of N, P, K, Ca, Mg, and Mn from decomposing litter.

## Materials and methods

### *Site description*

Three coniferous ecosystems, Douglas-fir, western hemlock

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(*Tsuga heterophylla* (Raf.) Sarg.), and Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) and one deciduous ecosystem, red alder (*Alnus rubra* Bong.), were selected. The Douglas-fir (45-year-old), western hemlock (70-year-old), and red alder (45-year-old) stands were located within 1 km of each other at the A. E. Thompson Research Center of the College of Forest Resources, University of Washington. The Thompson site is located at an elevation of 210 m, approximately 50 km east of Seattle in the City of Seattle's Cedar River Watershed, Washington, U.S.A. The Pacific silver fir stand was 175 years old and was located at Findley Lake in the upper Cedar River Watershed at an elevation of 1150 m, approximately 85 km east of Seattle. Mean annual rainfall at the Thompson site is 144 cm with a winter maximum. At Findley Lake mean annual rainfall is 273 cm. Most of the precipitation at Findley Lake is in the form of snow which may cover the forest floor for as long as 9 months. Mean annual air temperatures at the Thompson site and Findley Lake are 9.4 and 5.4°C, respectively.

Soils in the Douglas-fir and western hemlock stands are a gravelly loamy sand derived from glacial outwash material (Grier and McColl 1971). The soil in the red alder stand is a sandy loam of the Alderwood series (Cole and Gessel 1968). In the Pacific silver fir stand soils are derived from volcanic ash overlying andesitic glacial till (Ugolini et al. 1977). The thickness of the forest floor varied between 1.5-3.0 cm in the red alder and Douglas-fir stands, 3.5-6.0 cm in the western hemlock stand, and 5.0-9.0 cm in the Pacific silver fir stand.

Understory vegetation in the Douglas-fir stand is dominated by salal (*Gaultheria shallon* Pursh.), while sword fern (*Polystichum munitum* (Kaulf.) Presl) dominates in the red alder stand. There is very little understory vegetation in the western hemlock stand but sword fern and moss do occur. In the Pacific silver fir stand primary understory species are beargrass (*Xerophyllum tenax* (Pursh.) Nutt), big leaf huckleberry (*Vaccinium membranaceum* Dougl. ex Hook.), and ovalleaf huckleberry (*Vaccinium ovalifolium* Smith).

### *Needle and leaf litter decomposition*

The extent of needle decomposition was determined using the nylon mesh bag technique. Litterbags were 25.4 cm × 17.8 cm (0.045 m$^2$) with a mesh size of 1.0 mm (Nylon Net Co., Tennessee). Witkamp and Olson (1963) found 1-mm mesh size litterbags to underestimate true decomposition rates because of exclusion of large soil invertebrates. However, research by the author (unpublished) has shown that the 1-mm mesh size does not exclude the more important small invertebrates in the forest ecosystems studied here.

In the fall of 1974 canvas sheets were placed in each stand and needle and leaf litter was collected. This is the peak period of needle and leaf litter fall in Northwest forests (Gessel and Turner 1974, 1976). The litter collected was air dried; ovendry weight (48 h at 75°C) was then determined on a subsample. The equivalent of 10 g ovendry weight of litter was placed in each bag. This litter weight per unit area of litterbag falls within the range of annual litter fall weights per unit area of forest floor occurring in Northwest forests.

Square (0.045 ha) study plots were located in each stand on relatively level terrain. A 5 m × 5 m area was laid out in each plot and litterbags were placed in a randomized block design within this area. Bags were placed on November 15, 1974, in the Pacific silver stand and December 17, 1974, in the stands at the Thompson site. Only litter native to each site was returned to each site. Five bags were randomly sampled at each collection time, i.e., 3, 6, 12, and 24 months after placement at the Thompson site and 6, 9, 14, and 24 months at Findley Lake. The irregular schedule at Findley Lake occurred because deep snow prevented access to litterbags in winter. Litterbags were transported to the laboratory and dried immediately at 75°C to constant weight.

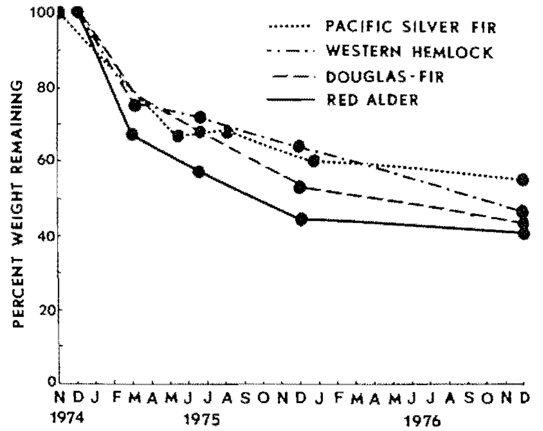

FIG. 1. Percent weight loss of Pacific silver fir, Douglas-fir, and western hemlock needles and red alder leaves in relation to time.

### *Chemical analyses*

Three of the five replicate litterbags collected at each sample time were randomly selected for chemical analyses. Litter was ground in a Wiley mill to pass through a No. 20 stainless steel mesh screen. Ground litter was digested using the wet oxidation method (Parkinson and Allen 1975). Nitrogen and P concentrations were then determined on an autoanalyzer (Technicon, auto analyzer II). Concentrations of P, Ca, Mg, and Mn were determined using an atomic absorption spectrophotometer (IL 353). Carbon was determined by a dry combustion technique on a Leco carbon analyzer. Ratios of C to N were calculated. Absolute weights of elements in the litterbags were calculated in grams per square metre as follows: (element concentration (parts per million)/$10^6$ × current ovendry weight (grams))/litterbag area (0.045 m$^2$). Lignin and cellulose were determined for the initial and 24-month samples using the Van Soest (1963) technique.

### *Temperature and moisture determinations*

Air temperatures at the Thompson site were determined weekly to the nearest degree Celsius with shielded maximum-minimum thermometers (Taylor) placed approximately 30 cm above the forest floor in each stand. Litter temperatures at the midpoint of the litter layer were also determined weekly using a Taylor probe thermometer. At Findley Lake air and litter temperatures were determined using thermistors. Millivolt signals were recorded on a Metrodata data logger. At each site litter (L and F layers) moisture was determined gravimetrically from three random samples taken monthly and expressed on a wet weight basis after drying at 75°C for 48 h.

### *Determination of litter decomposition constant (*k*)*

The decomposition constant ($k$) was determined by using Olson's (1963) equation, $X = X_0e^{-kt}$, where $X_0$ = initial weight of needles in the litterbags and $X$ = weight of needles after time $t$ (years).

## Results

### *Decomposition rates in the four ecosystems*

Needle and leaf weight loss varied from 37.4 to 55.1% in the four ecosystems after 1 year and from

TABLE 1. Weight loss ± standard deviation and decomposition constants after 1 and 2 years for red alder leaves and Douglas-fir, western hemlock, and Pacific silver fir needles

| Ecosystem | Weight loss, % | | Decomposition constant $k^a$, years$^{-1}$ | |
|---|---|---|---|---|
| | Year 1 | Year 2 | Year 1 | Year 2 |
| Red alder | 55.1±2.6[b] | 58.5±5.5 | 0.82±0.04[b] | 0.45±0.07 |
| Douglas-fir | 46.5±4.4 | 56.3±9.5 | 0.63±0.08 | 0.44±0.14 |
| Western hemlock | 37.4±5.2 | 53.1±8.8 | 0.45±0.07 | 0.38±0.10 |
| Pacific silver fir | 41.2±1.7[c] | 45.3±1.7 | 0.45±0.03 | 0.30±0.02 |

[a] Based on litterbag weight loss calculated according to Olson (1963).
[b] Significant difference at the 99% level; LSD = 8.3 (weight loss), 0.13 ($k$ values) between ecosystems.
[c] Based on 14 months' decomposition.

45.3 to 58.5% after 2 years (Table 1, Fig. 1). Fastest decomposition after 2 years occurred with red alder leaves followed by Douglas-fir, western hemlock, and Pacific silver fir needles. Although there were significant differences in weight loss between the litter species in the three lowland stands after 1 year, there were no significant differences after 2 years. Red alder leaves showed rapid decomposition in the 1st year but decomposed little in the 2nd year. After 2 years red alder leaves and Douglas-fir needles had quite similar weight loss. Western hemlock needles and Pacific silver fir needles had similar weight loss after 1 year (Table 1), but after 2 years Pacific silver fir needles had lost less weight than western hemlock needles. These decomposition trends are also reflected in the decomposition constants ($k$ values) in Table 1. After 2 years $k$ values varied from 0.30 for Pacific silver fir needles to 0.45 for red alder leaves. Values of $k$ determined after 1 year were larger than those determined after 2 years.

### *Decomposition as a function of season*

Seasonal rates of decomposition in the various ecosystems are shown in Fig. 1. There was an initial large loss of litter weight in the first 6 months with 42.1, 22.7, 28.1, and 33.4% weight loss occurring in the red alder, Douglas-fir, western hemlock, and Pacific silver fir ecosystems, respectively. This initial loss no doubt included some leaching losses (Nykvist 1963). Although winter air temperatures were extremely cold in the Pacific silver fir ecosystem (Table 2), snow insulated the forest floor and allowed decomposition to proceed. Weight loss of Pacific silver fir needles in the cold period was greater than that for Douglas-fir and western hemlock needles. Decomposition occurred in the summer and fall months in all the lowland ecosystems although it was less than that occurring in the first 6 months. Greatest weight loss in the 6- to 12-month period occurred with Douglas-fir needles (13.8%) followed by red alder leaves (13.0%) and western hemlock needles (9.3%). No measurable decomposition was observed in the Pacific silver fir ecosystem in the early summer and weight loss in the 6- to 12-month period was lowest in this ecosystem (7.8%).

### *Temperature and moisture conditions*

Average annual air temperature was lowest in the Pacific silver fir stand (5.8°C; Table 2). Air temperature fluctuations were also greatest in this stand (−17 to 27°C). Highest air temperatures were recorded in the red alder stand (34°C). Maximum and minimum litter temperatures were similar in all stands despite differences in air temperature and ranged from −2.8 to 18.3°C. Litter temperatures in the Pacific silver fir stand did not vary as much as air temperatures because of the insulating effect of the snow pack.

TABLE 2. Air and forest floor temperatures and litter moisture in red alder, Douglas-fir, western hemlock, and Pacific silver fir ecosystems during a 2-year period

| Ecosystem | Air temperature, °C | | | Forest floor temperature, °C | | Litter moisture, % | |
|---|---|---|---|---|---|---|---|
| | Average annual | Maximum | Minimum | Maximum | Minimum | Average annual | Minimum |
| Red alder | 9.6 | 34.0 | −6.0 | 16.1 | −1.7 | 74 | 57 |
| Douglas-fir | 8.0 | 29.0 | −6.0 | 17.2 | −2.2 | 65 | 36 |
| Western hemlock | 9.5 | 30.0 | −7.0 | 18.3 | −2.8 | 66 | 32 |
| Pacific silver fir | 5.8 | 27.0 | −17.0 | 16.0 | −2.0 | 65 | 39 |

TABLE 3. Multiple stepwise linear regression equations relating the dependent variable $k$ (decomposition constant determined after 2 years) and independent litter quality and environmental variables. Correlation coefficients ($r$) are also shown

| Ecosystem | Regression equation | Correlation coefficient, $r$ |
|---|---|---|
| All stands | $k = 0.51 + 0.0069\text{MIA}^{a} - 0.00084C^{b}$ | 0.99 |
| Conifers | $k = 0.48 + 0.01\text{MIA}$ | 0.98 |
| Thompson site (red alder, Douglas-fir and western hemlock) | $k = 3.21 - 0.15\text{MAL}^{c}$ | 0.99 |

[a] MIA, minimum air temperature.
[b] $C$, C:N ratio.
[c] MAL, maximum litter temperature.

The red alder stand had the highest average and minimum litter moisture (74 and 57%, respectively; Table 2). Litter moisture was similar in the three coniferous stands. The Pacific silver stand had the highest minimum moisture (39%) followed by the Douglas-fir (36%) and western hemlock (32%) stands.

### *Lignin and cellulose concentration in the litter*

Western hemlock needles had the highest initial lignin concentration (35.5 ± 0.8% standard deviation), while Douglas-fir had the lowest (18.3 ± 1.0%). Red alder leaves (20.8 ± 1.5%) and Pacific silver fir needles (25.4 ± 0.2%) were intermediate. After 2 years' decomposition the lignin concentration in the litter had increased and averaged 36.0 ± 3.8, 42.7 ± 4.1, 43.8 ± 2.6, and 47.7 ± 2.6% for the western hemlock, and Douglas-fir needles, red alder leaves and Pacific silver fir needles, respectively. Initial cellulose concentrations were similar in all ecosystems ranging from 19 to 24%, and had changed little after 24 months' decomposition (ranging from 21.4 to 27.3%).

### *Relationships between decomposition rates and litter quality and environmental variables*

Average decomposition constants ($k$ values) based on 2 years' data were regressed against the environmental variables shown in Table 2 (air temperature, forest floor temperature, and litter moisture) and the litter quality variables (C:N ratio and percent lignin). Simple and multiple stepwise linear regression analyses were used.

When all stands and conifer stands only were considered, $k$ values were most strongly related to minimum air temperature ($r = 0.97$ and 0.98, respectively). In the Thompson site stands $k$ values were strongly related to maximum and minimum litter temperatures ($r = 0.99$ for both). Litter moisture was poorly correlated with $k$ values except for the Thompson site data where minimum litter moisture used as the independent variable resulted in an $r$ value of 0.93.

The $k$ values were better related to C:N ratios ($r = -0.95$ for all stands, $r = -0.96$ for conifers, and $r = -0.98$ for the lowland stands) than percent lignin, in which case $r$ values ranged from $-0.20$ to $-0.78$.

Use of multiple stepwise linear regression analyses produced the equations shown in Table 3. For all stands minimum air temperature combined with the C:N ratio produced an $r$ value of 0.99. On the other hand when conifer ecosystems alone were considered the highest $r$ value resulted with minimum air temperature alone. When only Thompson site stands were considered maximum litter temperature was the independent variable resulting in the highest $r$ value ($r = 0.99$).

### *Release of nutrients from litterbags*

#### *Nitrogen*

The N concentrations of all needles and leaves increased in comparison to the initial concentrations throughout the 24-month period (Table 4). Maximum N concentration was 2.49% in red alder leaves after 12 months.

Patterns of N release in the needles and leaves differed markedly from ecosystem to ecosystem as decomposition progressed (Fig. 2*a*). In the red alder ecosystem N amounts in the leaves decreased continuously over the 2-year period. In the conifers amounts of N decreased slightly in Douglas-fir needles after an initial increase, remained about the same in western hemlock needles and more than doubled in Pacific silver fir needles after 2 years.

#### *C:N ratios*

The C:N ratio in the red alder leaves fell from 31.5 to 19.6 after 6 months and then essentially remained constant (Table 4). Patterns of change in the C:N ratio with time were different in the conifer needles. In the Douglas-fir, western hemlock, and Pacific silver needles, C:N ratios gradually decreased from 49.8 to 23.9, from 83.6 to 36.7, and

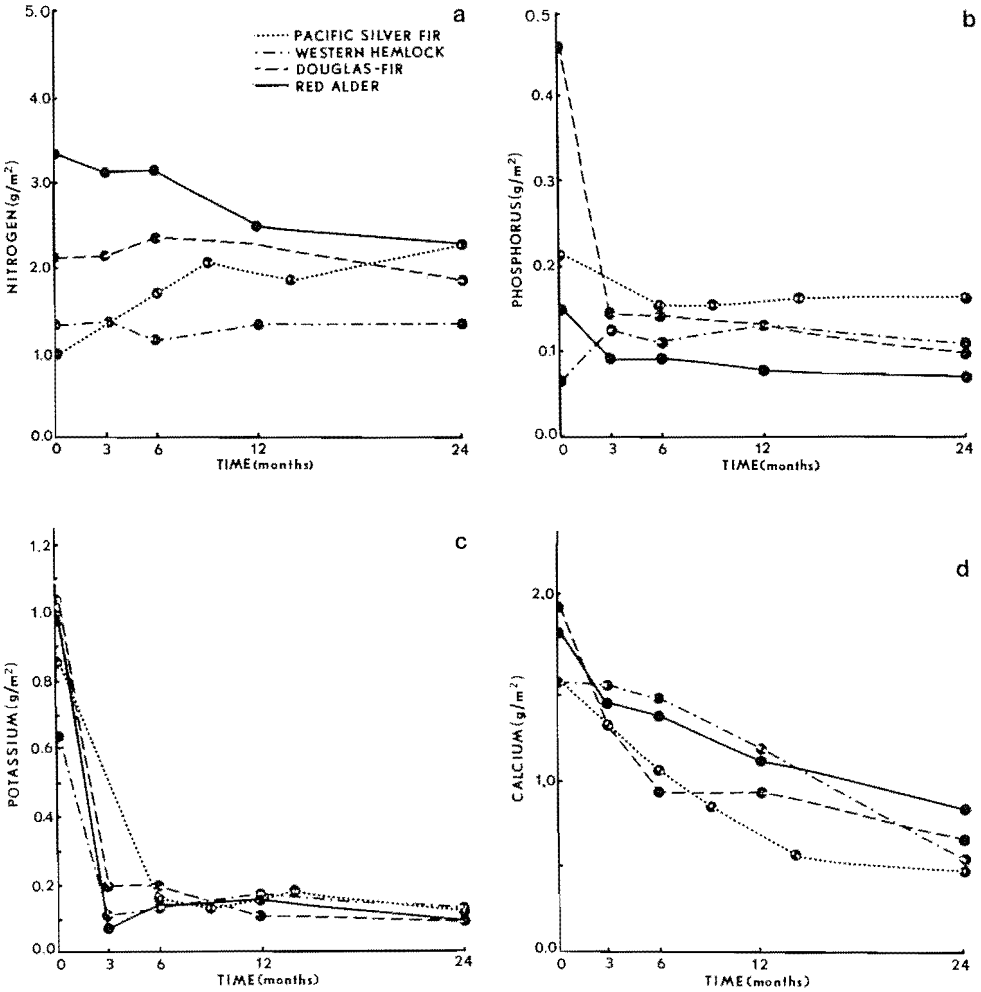

FIG. 2. Weights (grams per square metre) of (*a*) nitrogen, (*b*) phosphorus, (*c*) potassium, and (*d*) calcium in litterbags after 3, 6, 12, and 24 months' decomposition in Pacific silver fir, western hemlock, Douglas-fir, and red alder ecosystems.

from 110.0 to 28, respectively, throughout the 2-year period.

*Phosphorus*

Phosphorous concentrations after 2 years' decomposition remained about the same in red alder leaves, increased in western hemlock and Pacific silver fir needles, and decreased in Douglas-fir needles (Table 4).

Absolute amounts of P in the red alder, Douglas-fir and Pacific silver fir litter had decreased after 2 years, but accumulation had occurred in the western hemlock litter (Fig. 2*b*). Rapid loss of P occurred during the first 3 months of Douglas-fir needle decomposition.

*Potassium*

Potassium concentrations in the red alder leaves and Douglas-fir, western hemlock, and Pacific silver fir needles dropped quickly in the first 3 months and then stabilized (Table 4). This trend is particularly apparent when absolute amounts of K are considered (Fig. 2*c*).

*Calcium*

Calcium concentrations after 2 years' decomposition had increased slightly in red alder leaves and decreased in the conifer needles (Table 4). Greatest decrease occurred in the Pacific silver fir needles. Absolute amounts of Ca in all needles and leaves decreased steadily over the 2-year decomposition period (Fig. 2*b*).

*Magnesium and manganese*

Magnesium concentrations had decreased after 2 years' decomposition in the red alder leaves and Douglas-fir and Pacific silver fir needles (Table 4), but had increased in the western hemlock needles

TABLE 4. Nutrient concentrations (± standard deviation) of red alder leaves, and Douglas-fir, western hemlock, and Pacific silver fir needles in litterbags in relation to time

| Collection date, month · day · year | Ecosystem | Duration of decomposition, months | Dry weight, g | C, % | N, % | C:N | P, ppm | K, ppm | Ca, ppm | Mg, ppm | Mn, ppm |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 11 · 15 · 74 | Pacific silver fir | 0 | 10.0 | 49.5 | 0.45 | 110.0 | 962 | 3881 | 7122 | 1059 | 784 |
| 12 · 17 · 74 | Red alder | 0 | 10.0 | 47.9 | 1.52 | 31.5 | 690 | 4440 | 8070 | 1530 | 240 |
|  | Douglas-fir | 0 | 10.0 | 46.8 | 0.94 | 49.8 | 2080 | 4710 | 8660 | 850 | 1450 |
|  | Western hemlock | 0 | 10.0 | 48.5 | 0.58 | 83.6 | 290 | 3000 | 7000 | 500 | 790 |
| 3 · 14 · 75 | Red alder | 3 | 6.70(0.20) | 48.1(0.8) | 2.10(0.24) | 22.9 | 595(71) | 1259(121) | 9774(1517) | 1253(265) | 262(52) |
|  | Douglas-fir | 3 | 7.73(0.11) | 45.7(3.8) | 1.26(0.03) | 36.2 | 821(31) | 399(52) | 7707(286) | 353(25) | 459(35) |
|  | Western hemlock | 3 | 7.58(0.32) | 48.5(1.3) | 0.82(0.38) | 59.1 | 726(233) | 622(159) | 9330(279) | 745(137) | 1636(136) |
| 5 · 24 · 75 | Pacific silver fir | 6 | 6.66(0.15) | 49.8(0.6) | 1.18(0.13) | 42.2 | 1046(99) | 1060(123) | 7137(1943) | 519(80) | 606(101) |
| 6 · 30 · 75 | Red alder | 6 | 5.79(0.43) | 48.4(0.4) | 2.47(0.09) | 19.6 | 683(37) | 1555(374) | 10709(970) | 1445(203) | 231(11) |
|  | Douglas-fir | 6 | 6.73(0.13) | 46.3(0.2) | 1.60(0.04) | 28.9 | 958(193) | 997(248) | 6297(1418) | 384(83) | 457(93) |
|  | Western hemlock | 6 | 7.19(0.81) | 48.4(0.6) | 0.74(0.02) | 65.4 | 650(55) | 854(132) | 9296(352) | 529(61) | 1470(1139) |
| 8 · 20 · 75 | Pacific silver fir | 9 | 6.88(0.32) | 50.5(0.6) | 1.36(0.04) | 37.1 | 988(25) | 856(132) | 5497(740) | 423(52) | 673(212) |
| 12 · 17 · 75 | Red alder | 12 | 4.49(0.26) | 48.0(0.9) | 2.49(0.20) | 19.3 | 773(44) | 1080(39) | 11157(193) | 1496(40) | 641(6) |
|  | Douglas-fir | 12 | 5.35(0.44) | 47.0(0.4) | 1.90(0.11) | 24.7 | 1082(46) | 1296(322) | 7835(107) | 916(251) | 762(127) |
|  | Western hemlock | 12 | 6.26(0.52) | 48.7(0.7) | 0.96(0.04) | 50.7 | 921(108) | 1178(154) | 8463(664) | 811(113) | 1171(88) |
| 1 · 8 · 76 | Pacific silver fir | 14 | 5.88(0.47) | 49.4(0.8) | 1.45(0.10) | 34.1 | 1213(55) | 1379(100) | 4396(771) | 448(3) | 720(26) |
| 11 · 19 · 76 | Pacific silver fir | 24 | 5.47(0.17) | 51.5(0.2) | 1.84(0.11) | 28.0 | 1314(159) | 1092(91) | 3932(225) | 504(62) | 775(139) |
| 12 · 16 · 76 | Red alder | 24 | 4.15(0.55) | 48.0(0.2) | 2.45(0.03) | 19.6 | 786(47) | 1060(248) | 9076(339) | 1027(38) | 470(13) |
|  | Douglas-fir | 24 | 4.37(0.95) | 45.1(0.9) | 1.89(0.11) | 23.9 | 1024(139) | 926(279) | 6862(409) | 765(81) | 1391(164) |
|  | Western hemlock | 24 | 4.69(0.88) | 47.0(0.5) | 1.28(0.31) | 36.7 | 1054(174) | 1308(226) | 5165(1110) | 619(138) | 2833(1449) |

TABLE 5. Relative elemental mobility after 2 years in comparison to initial content in decomposing red alder leaves, and Douglas-fir, western hemlock, and Pacific silver fir needles

| | |
|---|---|
| Red alder | K > Mg > Ca > P > N > Mn |
| Douglas-fir | K > P > Ca > Mg > Mn > N |
| Western hemlock | K > Ca > Mg > N > Mn > P |
| Pacific silver fir | K > Mg > Ca > Mn > P > N |

after 2 years. Concentrations of Mn had increased in red alder leaves and western hemlock needles after 2 years' decomposition (Table 4) but remained about the same in Douglas-fir and Pacific silver fir needles. Magnesium content had also increased in western hemlock needles after 2 years' decomposition.

*Element mobility series*

Table 5 shows a mobility series for N, P, K, Ca, Mg, and Mn in the various ecosystems after 2 years' decomposition. Potassium was the most mobile element in all ecosystems. Nitrogen was the least mobile element in the Douglas-fir and Pacific silver fir ecosystems and the second least mobile element in the red alder ecosystem. Relatively, N was most mobile in the western hemlock ecosystem. Phosphorus was more mobile than N in the Douglas-fir, red alder, and Pacific silver fir ecosystems, particularly in the Douglas-fir ecosystem. On the other hand N was more mobile than P in the western hemlock ecosystem. Calcium and Mg tended to have intermediate mobility.

## Discussion

*Litter decomposition rates*

Litter decomposition rates decreased in the following sequence; red alder leaves and Douglas-fir, western hemlock, and Pacific silver fir needles. After 2 years' decomposition, however, differences in decomposition rates were not statistically significant, although significant differences did occur after 1 year.

Rates of decomposition of red alder leaves after 1 year ($k = 0.82$) were similar to those obtained for yellow birch at Hubbard Brook, New Hampshire ($k = 0.85$), but were greater than those for sugar maple and beech leaves ($k = 0.51$ and 0.37, respectively, Table 6). Table 6 compares litter decomposition rates in a variety of forest ecosystems. Lousier and Parkinson (1976) compiled $k$ values for a variety of deciduous litters and found $k$ values ranging from 0.11 for *Populus tremuloides* to 1.15

TABLE 6. Comparison of annual decomposition constant ($k$) for selected coniferous and deciduous leaf litters

| Site | Tree species | $k$ | Reference |
|---|---|---|---|
| | | Coniferous | |
| Findley Lake, WA | *Abies amabilis* | 0.56 | Turner and Singer (1976) as reported by Fogel and Cromack (1977) |
| Findley Lake, WA | *Abies amabilis* | 0.30 | This study |
| Wildcat Mt. OR | *Abies procera* | 0.31 | Fogel and Cromack (1977) |
| Oak Ridge, TN | *Pinus* sp. | 0.45 - 0.58 | Sollins et al. (1973) |
| Coweeta, NC | *Pinus* sp. | 0.42 - 0.52 | Cromack (1973) |
| Finland | *Pinus* sp. | S, 0.43; N, 0.31 | Mikola (1960) |
| New Zealand | *Pinus* sp. | 0.36 | Will (1967) |
| Blue River, OR | *Pseudotsuga menziesii* | 0.22 - 0.32 | Fogel and Cromack (1977) |
| Philomath, OR | *Pseudotsuga menziesii* | 0.35[a] | Fogel and Hunt (1979) |
| Wildcat Mt., OR | *Pseudotsuga menziessii* | 0.38 | Fogel and Cromack (1977) |
| Cedar River, WA | *Pseudotsuga menziessii* | 0.40 - 0.56 | Edmonds (1979) |
| Cedar River, WA | *Pseudotsuga menziessii* | 0.44 | This study |
| Alaska | *Picea glauca* | 0.22 | Piene and Van Cleve (1978) |
| Cedar River, WA | *Tsuga heterophylla* | 0.38 | This study |
| | | Deciduous | |
| Hubbard Brook, NH | *Acer saccharum* | 0.51[a] | Gosz et al. (1973) |
| Cedar River, WA | *Alnus rubra* | (0.82)[a] 0.45 | This study |
| Alaska | *Alnus crispa* | 0.41 - 0.42 | Van Cleve (1971) |
| Hubbard Brook, NH | *Betula allegheniensis* | 0.85[a] | Gosz et al. (1973) |
| England | *Corylus avellana* | 0.60[a] | Bocock (1963) |
| Hubbard Brook, NH | *Fagus grandifolia* | 0.37 | Gosz et al. (1973) |
| Canada | *Populus tremuloides* | 0.11 - 0.49 | Lousier and Parkinson (1976) |
| Canada | *Populus balsamifera* | 0.12 - 0.49 | Lousier and Parkinson (1976) |

[a] Based on 1 year's decomposition.

for *Cornus florida*. Red alder would thus appear to have an intermediate decomposition rate.

Bocock (1963) examined leaf decomposition rates of another alder species (*Alnus glutinosa*) in England. Unfortunately he did not present data for a whole year. However, leaves of this species appear to decompose faster than red alder leaves. He found weight losses ranging from 70 to 90% after 8 months. In this study red alder leaves lost only 55% of their initial weight after 1 year. Van Cleve (1971), examined decomposition of *Alnus crispa* leaves in Alaska and found $k$ values similar to those for red alder leaves in this study (Table 6).

Decomposition rates of Douglas-fir needles after 2 years ($k$ = 0.44) were slightly higher than those found by Fogel and Cromack (1977) for Douglas-fir needles in old-growth stands in Oregon ($k$ = 0.22-0.38). Edmonds (1979) had previously determined that litter decomposition rates were faster in young-growth Douglas-fir ecosystems in Washington as shown in Table 6. Fogel and Hunt (1979), however, in a young-growth Douglas-fir stand in Oregon calculated a $k$ value of only 0.35. Rates for Douglas-fir are similar to those reported for pine ecosystems in the eastern United States and in South Finland (Table 6).

The decomposition rates of *Abies amabilis* needles at Findley Lake ($k$ = 0.30) were almost identical to those found for *Abies procera* needles at Wildcat Mountain, Oregon (Table 6). Both ecosystems are snow covered in winter. Fogel and Cromack (1977), however, calculated a higher $k$ value (0.56) for Pacific silver fir needles at Findley Lake from data reported by Turner and Singer (1976). In general, needle decomposition rates in snow covered ecosystems in Oregon and Washington needles are considerably higher than those reported for *Picea glauca* in Alaska (Table 6).

The 1st-year litter decomposition patterns determined in this study were similar to those found by Vogt et al. (1980) in a later study; however, they found that Pacific silver fir needles had decomposed slightly slower than western hemlock needles after 12 months.

### *Factors influencing litter decomposition*

Litter decomposition is largely controlled by temperature, moisture and chemical composition of the litter. Needle decomposition rates were found to be strongly related to litter moisture in Douglas-fir ecosystems by Edmonds (1979) and Fogel and Cromack (1977). A summer drought generally occurs in these ecosystems. However, over the range of ecosystems considered in this study, $k$ after 2 years was most strongly related to minimum air temperature.

The regression analyses, however, used averages over a 2-year period as independent variables. This may mask variables important in controlling decomposition on a seasonal basis.

Seasonal decomposition patterns in the four ecosystems in the 1st year are shown in Fig. 1. Decomposition rates were slow in the summer particularly in the Pacific silver fir ecosystem. Vogt et al. (1980) also found a similar summer decomposition pattern in the four ecosystems. Regression analyses revealed that average $k$ values after 1 year were better related to average and minimum litter moisture ($r$ = 0.85 for both) than any temperature variable. Even stronger relationships may have resulted if moisture content of the fresh litter had been used instead of moisture content of the L plus F layers.

Although the Pacific silver fir ecosystem was covered with snow in the winter, decomposition still proceeded (Fig. 1). In fact decomposition in the first 6 months was faster in the Pacific silver fir ecosystem than in the lowland coniferous ecosystem. The forest floor was not frozen and remained at a constant temperature of 0.5°C while the snow pack cover was in place. This no doubt created a more favorable condition for the microbes than the fluctuating winter temperatures experienced in the lowland ecosystems where diurnal freezing and thawing occurred more frequently.

Litter quality also plays a large role in determining decomposition rates. Lignin has been suggested as a primary variable controlling decomposition (Fogel and Cromack 1977; Meentemeyer 1978). In this study $k$ values seemed better related to C:N ratios ($r = -0.95$ to $-0.98$) than to initial lignin content of the litter ($r = -0.20$ to $-0.78$). Fogel and Cromack (1977), however, used various substrates (needles, cones, bark, and branches) ranging widely in lignin content from 21.8 to 58.6%. The range of lignin concentrations was narrower in this study (18.3 to 35.3%). Also the lignin concentrations of red alder leaves and Pacific silver fir needles are similar (20.8 and 25.4, respectively), while their C:N ratios are widely different (31.5 and 110.3, respectively). Daubenmire and Prusso (1963) also found no relationship between lignin content and foliage litter decomposition rates in a laboratory study which involved a variety of western species including Douglas-fir and western hemlock.

### *Nutrient release from decomposing litter*

Many workers (Bocock 1963; Gosz et al. 1973; Will 1967; Edmonds 1979) have noted increased N concentrations in needles and leaves during the decomposition process. Similar results were found in this study. However, although the litter substrates increased in N concentration not all increased in absolute N content (Fig. 2*a*). Nitrogen was lost continuously from the red alder leaves during the decomposition process. On the other hand Douglas-fir needles initially gained and then lost N. This increase followed by a decrease was also observed by Edmonds (1979), Gosz et al. (1973), Lousier and Parkinson (1978), and Will (1967). The absolute amount of N in the western hemlock needles changed little in the 2-year period while it continued to increase in the Pacific silver fir needles.

This N increase probably arises from external sources such as precipitation and insect frass in combination with fungal immobilization (Gosz et al. 1973). Fungal immobilization of N does occur in these Northwest United States forest ecosystems as evidenced by concentrations of N in fleshy basidiomycete fruiting bodies. Highest mean levels of N occur in fruiting bodies in the Pacific silver fir ecosystem (3.2%) in comparison to 2.7 and 2.9% in the western hemlock and Douglas-fir ecosystems, respectively (Vogt and Edmonds 1980). Also N levels in the forest floor of the Pacific silver fir ecosystem are considerably higher (1.3%) than those in the western hemlock (0.9%) and Douglas-fir (0.9%) ecosystems (Vogt and Edmonds 1980).

Mineralization of N from litter has traditionally been related to the C:N ratio. Lutz and Chandler (1946) indicate that N mineralization should occur at C:N ratios between 20:1 and 30:1. Above these levels microbial immobilization occurs.

In the red alder ecosystem N mineralization commenced immediately after the leaves were placed on the forest floor when the C:N ratio was 31.5. It began in the Douglas-fir ecosystem when the C:N ratio dropped below 28.9 (after 6 months). Edmonds (1979) found in other Douglas-fir stands that mineralization started when the C:N ratio was between 23:1 and 35:1. At the end of the 2-year period no N mineralization had occurred in either the western hemlock or Pacific silver fir needles. The C:N ratio in the western hemlock needles was 37:1 at the end of 2 years so the lack of N mineralization was not surprising. On the other hand the C:N ratio in the Pacific silver fir ecosystem had fallen to 28:1 after 2 years so some mineralization might have been expected. The C:N ratio at which N mineralization occurs thus appears to vary between ecosystems but appears to be somewhere between 23:1 and 35:1 as previously indicated by Edmonds (1979).

Greatest loss of N from decomposing litter was noted in red alder leaves with 67% remaining after 2 years. In the Douglas-fir needles, 88% of the initial N remained. Edmonds (1979) noted, however, that this may vary from one Douglas-fir ecosystem to another. For example in a 24-year-old Douglas-fir stand, 70% of the initial N remained in needles after 2 years and this is very similar to that for red alder leaves.

Phosphorous release patterns from the litter also varied markedly between ecosystems (Fig. 2*b*). Rapid release of P occurred in the first 3 months from Douglas-fir litter while less rapid release was observed from the Pacific silver fir and red alder litter. In all three of these cases the most rapid release occurred in the first 3 months. The situation with the western hemlock needles was quite different, however, with an increase in absolute P amounts in the litter the first 3 months followed by little change in the next 21 months. Gosz et al. (1973) found an increase in absolute weights of P during the 1st year of decomposition.

Critical ratios have also been proposed for P mineralization. Alexander (1977) has suggested that P mineralization begins when C:P ratios are between 100:1 and 300:1. Lousier and Parkinson (1978) suggested a critical ratio of 230:1 for aspen and balsam leaf litter. Initial C:P ratios in this study were 255:1, 574:1, 694:1, and 1672:1 for Douglas-fir, red alder, Pacific silver fir, and western hemlock litter, respectively. After 2 years these ratios had changed to 440:1, 392:1, 610:1, and 445:1 for the same litter sequence.

Douglas-fir litter had an initial C:P ratio which would allow mineralization which would explain the initial loss of P from the Douglas-fir needles (Fig. 2*b*). However, it is apparent that mineralization can proceed at higher C:P ratios than those suggested by Lousier and Parkinson (1978). Fungal immobilization of P has been observed in all these ecosystems (Vogt and Edmonds 1980).

Calcium was lost steadily throughout the 24-month period in all ecosystems. It appears that decomposition is responsible for most of the Ca loss. There was no fungal immobilization of Ca observed in any of these ecosystems (Vogt and Edmonds 1980).

Increased Mn concentrations and contents occurred in western hemlock needles after 2 years. Cragg et al. (1977) with aspen leaves and Lousier and Parkinson (1978) with aspen and balsam leaves also found an absolute increase in Mn as decomposition proceeded. Manganese, however, was not accumulated by fungi in the western hemlock ecosystem (Vogt and Edmonds 1980). Lousier and Parkinson (1978) suggested that the same factors governing Fe increase hold for Mn, including foliar leaching, dust, green litterfall, weathering of parent material, etc.

Lousier and Parkinson (1978) have compiled element mobility series for a variety of forest ecosystems throughout the world, and from their compilation it appears generally that K is the most readily released element while N is the least mobile when considering only N, P, K, Ca, Mg, and Mn. There is, however, considerable variation in the arrangement of elements in mobility series from ecosystem to ecosystem as illustrated in this study.

Nitrogen was the least mobile element in the Douglas-fir and Pacific silver fir ecosystems while Mn and P were the least mobile in the red alder and western hemlock ecosystems, respectively (Table 5). Potassium was always the most mobile element in all ecosystems.

It can be concluded that litter decomposition rates and the pattern of nutrient release from decomposing litter can vary from ecosystem to ecosystem in the Pacific Northwest. Fastest decomposition occurred in the red alder ecosystem while the slowest was in the subalpine Pacific silver fir ecosystem. Intermediate decomposition rates occurred in Douglas-fir and western hemlock ecosystems. Decomposition constants were highly correlated with minimum air temperature and C:N ratios over the range of ecosystems studied. Low summer litter moisture and presence of an insulating snow cover for long periods, however, may strongly influence seasonal patterns of decomposition. The release of N from decomposing litter, in particular, varied from ecosystem to ecosystem. Nitrogen release was almost immediate from red alder leaves. On the other hand absolute amounts of N increased in Pacific silver fir needles over the 2-year study period. An understanding of the release of nutrient elements during the litter decomposition process along with the potential for fungal immobilization may help in explaining tree response to fertilization in Northwest forests.

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